DE GRUYTER MOUTON
DOI 10.1515/langcog-2013-0008 — Language and Cognition 2013; 5(2–3): 133–143

Klaus Zuberbühler

Acquired mirroring and intentional communication in primates

Abstract: Arbib offers a coherent proposal of how the brain has evolved to become language-capable. Integral to the argument are mirror neurons, cells discovered in macaque brains with interesting firing patterns, and studies on gestural communication of great apes. Here, I first discuss some complexities of the recent mirror neuron literature, which suggest that 'mirroring' may be an ontogenetically acquired, not an evolved, feature of neurons. Second, it is now clear that chimpanzee vocal behaviour is strongly mediated by social variables, and that individuals can use vocalisations to persuade and inform others, facts that have implications for gestural theories of language evolution. I conclude with discussing research most needed for making progress in understanding how human language has evolved.

Keywords: primate communication, mirror neuron, chimpanzee, language evolution, vocalisation

Klaus Zuberbühler: School of Psychology and Neuroscience, University of St Andrews, Scotland; Institute of Biology, Department of Comparative Cognition, University of Neuchatel, Switzerland. E-mail: kz3@st-andrews.ac.uk

1 Introduction

The evolution of language is often considered one of the hardest problems in science, and Michael Arbib is to be congratulated for putting forward a coherent story of how the human brain, the organ of language, could have evolved to become language capable. To understand its evolution, human language is perhaps best investigated as a collection of independent mechanisms with their own evolutionary histories. One way to make progress in this direction is by carrying out comparative studies that involve non-human primates, and Arbib makes ample use of primatological findings to advance his arguments. He follows a framework proposed by Hockett (1960), who has compiled a list of components that characterise language. Arbib's list contains 11 key properties, including complex action recognition and imitation, intentional communication, symbolisation, parity, displacement, and so on. An added feature is that, throughout the book,

Arbib is trying to convince the reader that the emergence of mirror neurons was a key evolutionary event towards language-capability, so this deserves special attention.

2 Mirror neurons: acquisition or inheritance?

Some cells in macaque brains respond to both observing and executing the same practical actions, such as grasping a peanut, and for this reason they have been named 'mirror neurons'. A rich interpretation of this neurobiological phenomenon is that mirror neurons do not just simply wire and fire together; they are not just intersections of motor and perceptual pathways, but play a governing role in cognition, for example by affording 'action understanding' and imitation (e.g. Rizzolatti and Craighero 2004), yielding first person insights into the intentions and goals of others (Gallese and Sinigaglia 2011), enabling theory of mind (Gallese and Goldman 1998), and, crucially, are required for language (Rizzolatti and Arbib 1998). Mirror neurons, in short, are the neural mechanism underlying a number of complex cognitive processes, many of which define human uniqueness.

Although these proposals have had much impact and intuitive appeal, I personally remain unconvinced that mirror neurons have done much in terms of advancing our understanding of language evolution, for a number of reasons. First, according to a recent review (Cook 2012), mirror neurons do not always mirror so well, but respond to similar, related, or even different actions in the observation and execution condition, with only a minority responding selectively when the subject observes and executes an action. Although firing rates can increase in both the observation and execution condition, they can also both decrease, or increase in one and decrease in the other condition (Mukamel et al. 2010).

Equally relevant is that 'mirroring' may not be a hardwired property, but a feature that can be acquired by a cell during ontogeny. This distinction is important because the current belief has been that mirror neurons are a species-specific property of some brains, with a tacit assumption that natural selection has favoured their evolution because of adaptive benefits in cognition. However, if mirror neurons are the result of ordinary learning processes, for example because visual and motor representations of actions are predictive of one another, then they should be found in response to any arbitrary event, provided the required contingencies are in place (Cook 2012). This hypothesis has some appeal if one considers that some of the actions tested with macaques involved 'unnatural' human artefacts (plastic crumbling, plier movements) instead of ecologically more relevant events as encountered by free-ranging macaques. If mirror neurons

are not the product of natural selection, but an acquired general feature of brain circuitry, then it is difficult to see why they should be given a privileged position in theories of language evolution (Heyes 2010).

Third, the best evidence for mirror neurons is still from single cell recordings in macaque brains, but these are primates that neither have language nor particularly impressive imitation abilities. Although it is likely that humans (and great apes) also have mirror neurons, it is less clear what we should conclude if mirror neurons turn out to be a general feature of vertebrate brains. For humans, Mukamel et al. (2010) recorded extracellular activity of cells in the medial frontal and temporal cortex while patients executed or observed hand grasping actions and facial emotional expressions. A significant proportion of neurons responded to both observation and execution of these actions, but a subset of these neurons showed excitation during execution and inhibition during observation, further suggesting that the current view of mirror neurons is too simplistic.

It is somewhat regrettable that Arbib does not address the current mirror neuron literature in its full complexity, particularly the key issues of ontogenetic flexibility and action specificity. As a result the reader is left with more questions and, in my case, remains unconvinced that mirror neurons should be granted a special place in the evolutionary theory of the language capable brain.

3 Primate communication and human language

Biologically, humans are primates, most closely related to chimpanzees and bonobos, with a shared common ancestor 7–8 million years ago, according to a recent estimate (Langergraber et al. 2012). Members of the genus *Homo* start appearing in the fossil record around 2 million years ago, while modern humans are only a few hundred thousand years old, a very short time period for major evolutionary transitions to occur. The key components of the human language faculty, in other words, are unlikely to have evolved 'ex nihilo' in such a short time, so what were the relevant precursors?

Arbib's scenario is that language evolved in two stages. Manual-based protolanguage came first, followed by a vocal-based protolanguage that came second. In support, Arbib discusses the fact that humans gesture when speaking, something that is also observed in blind people, while deaf people develop gestural communication in the absence of auditory input. Opponents of gesture-first theories typically argue that this scenario is non-parsimonious because it requires two major evolutionary transitions, one from vocal to gestural and a second one from gesture to speech. The alternative is that speech has evolved directly from vocal communication, with gestures playing a subsidiary role throughout.

There is some hope that primate communication research can move this debate forward. Studies on gestural communication in great apes have shown that gestures are common during play (e.g. Pika et al. 2005), sexual solicitation (Hobaiter and Byrne 2011) and intergroup encounters (Herbinger et al. 2009). What is also well established is that great apes take into account the attentional state of their recipients when producing gestures, a fact that has been given special status in support of gestural theories of language evolution (Tomasello 2008).

Less clarity exists on what actually should count as a gesture. As a result, recorded repertoire sizes can vary dramatically, even within the same study group. For example, Hobaiter and Byrne (2011) discriminated more than 60 gestures in the Sonso chimpanzee community of Budongo Forest, Uganda, while Roberts et al. (2012) only found half as many, a reflection of methodological differences. Hobaiter and Byrne (2011) have chosen the typical approach in gesture studies, which is to record any body or limb movement with no obvious physical effect, but then to exclude those that do not pass "strict criteria for intentionality" (Genty et al. 2009), which typically leads to excluding around 50% of observations. The contentious point here is that the intentionality criteria used to exclude behaviour are all based on subjective observer judgements. Roberts et al.'s (2012) approach has been somewhat more objective in that the supposed gestural signals were identified by their physical structure before relating them to eliciting context and recipient responses, which resulted in a much smaller repertoire.

So far, research on ape gesture has spectacularly failed to provide evidence that these signals convey anything about the external world, apart from the signaller's desire to engage in a particular activity, typically to play, have sex, or persuade a recipient to move. Also, there is little evidence that gestures are conventionalised signs that have been acquired as part of a cultural process. Pantomiming is conspicuously absent, apart from isolated anecdotes, and idiosyncratic gestures are typically seen in captive apes interacting with humans, suggesting that they are instrumentally conditioned responses that have been acquired in the context of feeding.

Nevertheless, Arbib favours the 'gesture first' scenario and part of his strategy is to discount primate vocal behaviour as irrelevant for questions of language evolution. In his view, primate vocalisations are not used intentionally "to influence the behaviour of specific others" (p. 74), while chimpanzees are "unable to suppress calls" and "vocal communication may not involve the caller's assessment of the recipient's knowledge". However, my reading of the current primate literature is that these points need to be revised, as there is good evidence for persuasion, inhibition and provision of information in great ape vocal communication. I will review some of the relevant evidence in the following sections.

3.1 Persuasion

In a study with wild chimpanzees, victims of social aggression produced acoustically distinct victim screams with a graded structure that reflected the nature of the attack experienced by the victim (Slocombe and Zuberbühler 2005). But in addition, the acoustic structure of these screams was further affected by the composition of the nearby audience: if victims were with other individuals who outranked the attacker, then they tended to produce screams shifted towards the severe end of the acoustic spectrum, as if trying to persuade these powerful bystanders to intervene on their behalf (Slocombe and Zuberbühler 2007).

Other evidence is from the foraging context. When encountering food, chimpanzees often produce specific, acoustically graded vocalisations, the so-called 'rough grunts'. Depending on the type of food encountered, the acoustic structure of these calls varies, broadly reflecting the caller's personal food preference (Slocombe and Zuberbühler 2006). However, callers are significantly more likely to produce 'rough grunts' if they travel with 'friends', i.e. group members with whom they have strong grooming relationships compared to 'non-friends' (Slocombe et al. 2010), suggesting that the decision to call largely depends on whether callers are with someone they want to feed with.

3.2 Inhibition

Contrary to what Arbib writes there is very clear evidence that chimpanzees can suppress calls, usually if they assess a social situation in an unfavourable way. For example, during sex females regularly, but not always, produce copulation calls. Calling frequency is independent of a female's identity or social position, but strongly determined by the rank of her male partner. With low-ranking males, females consistently suppress their copulation calls, in contrast to when copulating with a high-ranking male. In addition, females are significantly more likely to suppress calls if surrounded by large female audiences, while the size of the male audience has no effect (Townsend et al. 2008). The most likely explanation for such vocal inhibition is that females seek to minimise aggression. For instance, when caught copulating with low-ranking males females can be attacked by a high-ranking male. Similarly, there is considerable hostility between female chimpanzees (Townsend et al. 2007), suggesting that females seek to disguise their sexual behaviour from other females.

Inhibitory effects on vocal behaviour are also observed in other contexts, such as when low-ranking individuals encounter higher-ranking group members.

In the typical case, the lower-ranking individual produces a vocal 'greeting' signal, a so-called 'pant grunt', which facilitates peaceful interactions between the two, despite their rank differences. However, if the alpha male is in the vicinity, lower-ranking individuals are significantly less likely to greet high-ranking individuals, despite everything else being equal (Laporte and Zuberbühler 2010), providing further evidence that chimpanzee vocal behaviour is under considerable social control.

3.3 Informing

Perhaps the most important piece of evidence for arguments about language evolution concerns the question of whether non-human primates are capable of actively informing others about events in the world. Passive informing certainly exists in the form of recipients making inferences about the event type encountered by a caller, and Arbib acknowledges this fact. In the classic case, free-ranging vervet monkeys produce acoustically distinct alarm calls to different predators and recipients respond to these calls as if having spotted the corresponding predator themselves, for instance by running to cover when hearing another monkey's 'eagle' alarm call (Seyfarth et al. 1980). However, a monkey calling in response to an eagle may do so regardless of the state or composition of its audience.

Although predator-specific alarm calling has now been described for a range of primate and non-primate species (Zuberbühler 2011), such studies do not usually address whether the caller wishes to inform his audience about the event it has just perceived, or whether the calls are mere readouts of an underlying psychological state triggered by the event. In other words, the monkeys may simply communicate what they experience internally, without considering or including the composition and knowledge of their audience.

Although the final verdict is still out, a number of studies with monkeys have suggested that callers can be 'audience-aware' to various degrees. In one case, wild Thomas langur males were observed when alarm calling to a tiger model. The striking finding was that the males continued to alarm call until every group member had responded with at least one alarm call, as if trying to ensure that all group members were aware of the danger (Wich and de Vries 2006). Similarly, in a playback experiment male blue monkeys produced significantly more alarm calls if some of their own group members were close to a suspected predatory eagle compared to when the group was further away, while the calling male's *own* distance to the eagle had no effect (Papworth et al. 2008). Adult male primates often play an important role in protecting others from predation, which may explain their altruistic vocal behaviour in the presence of dangerous predators.

Fig. 1: Wild chimpanzees take into account their audience before vocalising to persuade others or inform them about relevant events (Photo Florian Möllers)

More directly relevant is a recent field experiment with wild chimpanzees. In this study, members of the Sonso community in Budongo Forest, Uganda, encountered a model of a dangerous viper. In response, individuals produced specific alarm calls ('alarm hoos'), but call production was significantly influenced by whether or not they were with group members who already knew about the snake. Again, this was independent of the caller's own experience with the snake, suggesting that chimpanzees take the knowledge state of their audience into account when producing warning calls (Crockford et al. 2012: Figure 1).

It is important to remember that the vocalisations investigated in these studies are part of a species-specific behavioural repertoire; they are not equivalent to speech signals. The calls will develop and appear in an animal's vocal repertoire, regardless of whether it happens to grow up in Uganda or the Ivory Coast. In humans, the basic speech units, the phonemes, are equally hard-wired but their combinatorial use is culturally acquired. What the primate studies show is that non-linguistic vocalisations are governed by psychological experiences, perhaps similar to what underlies and governs linguistic communication. Of course, it is

not possible for a chimpanzee to explain to another what it had for breakfast, or on which tree it spent the night, but it can indicate the location of food, inform others about danger, or choose to remain silent if social conditions are unfavourable.

4 Conclusion

Arbib must be congratulated for his ambitious project in trying to advance our understanding of how evolution made one primate brain capable of highly complex communication, language. What makes Arbib's approach different from other recent work on the same topic is that he is willing and able to discuss and review evidence from all levels of analysis, proximate mechanisms, ontogeny, biological function and phylogenetic history. How successful has he been with his mission?

It is natural that scholars differ in how they pick out empirical evidence when building their theories. Personally, I cannot get so excited over the fact that some cells in the macaque brain show interesting firing patterns, and the conceptual fabrications that have emerged from this. Maybe mirror neurons have emerged due to a chance mutation that has been favoured by natural selection because of enhanced cognitive abilities. However, the more typical case is that natural selection acts on entire organisms that are already well adapted to their current environments. I therefore find it more probable that mirror neurons are a natural biproduct of large brains, something that emerges ontogenetically as individuals learn how the world works.

In my opinion, progress on how the brain has become language-ready largely depends on two areas of research, the evolution of vocal control and the evolution of cooperative motivation. It is in these two areas where humans deviate most strongly from non-human primates. Whether one likes it or not, human language is largely a vocal behaviour, the product of an unusual motor skill that enables speakers to control their vocal tracts and its acoustic products in rapid and precise ways. In non-human primates, vocal tract control is only rudimentarily developed, with little evidence of vocal learning and influence of ontogenetic experience (Fitch and Zuberbühler 2013), although the basic vocal tract anatomy is largely identical. One way to make progress and to address this conundrum is to search for areas of enhanced vocal flexibility in modern primates, both within and between species and across functional contexts. For example, it has been found that vocal repertoire size correlates with social complexity in different primates (McComb and Semple 2005) suggesting that social evolution has been a main driving force towards enhanced vocal control. The sophisticated

vocal abilities of humans, according to this hypothesis, may have evolved due to especially complex social problems. This idea is supported by the fact that primate calls used in social interactions tend to be acoustically more variable than other calls. In great apes, acoustic gradation found in some calls has been linked with how individuals assess social situations (Slocombe and Zuberbühler 2005).

Another source of flexibility arises when primates produce sequences of calls, which can sometimes lead to changes in meaning (Arnold and Zuberbühler 2006; Ouattara et al. 2009), with some evidence also for great apes (Clay and Zuberbühler 2011). Although these phenomena are interesting, not enough material is currently available to decide whether primate call sequences are best described as a finite state grammar or whether they have basic hierarchical organisation, as is characteristic for human speech. It is also unclear how much control individuals have over sequence production and what role ontogeny and learning plays. Research is urgently needed in these areas.

A second major component of the language faculty, in my view, concerns the origins of the cooperative motivation that characterises human communication (Tomasello 2008, 2010). Unlike other primates, humans routinely base acts of communication on assumptions and knowledge that they share with receivers. The ability to take into account what information is novel and interesting for a receiver develops early in human infants, and may therefore not require advanced theory of mind abilities (Liebal et al. 2010). Primate communication and human language are thought to differ most fundamentally in this domain, although the demarcation between humans and primates appears to be fluid (Crockford et al. 2012). Very little systematic work has been done and it is therefore not possible to decide how important the ability to take others into account is in non-human primate communication.

How did humans evolve such a profoundly different way of communication compared to other primates? A key event after the split from the common ancestor was probably the migration out of the forested habitat, the home of most non-human primates, including all great apes. Survival and reproduction in the open savannah may have been more challenging for earlier humans due to predation, intergroup conflicts, and new demands in terms of cooperative breeding and foraging. Similar to meerkats and other social carnivores, the hominid response appears to have been to become hyper-social and hyper-cooperative. Equipped with an already very efficient communication device and high social skills, perhaps similar to what is seen in today's chimpanzees and bonobos, early humans were well positioned to evolve more efficient communication, characterised by enhanced vocal control and by a cognitive apparatus able to cope with a highly cooperative lifestyle.

The last mile to human uniqueness and language, therefore, can probably not be understood by comparative studies with non-human primates, but may require other approaches, such trying to understand the function of the genetic changes that have make us uniquely human (e.g. Enard et al. 2002).

References

Arbib, M. A. 2012. *How the brain got language*. Oxford: Oxford University Press.

Arnold, K. & K. Zuberbühler. 2006. Language evolution: Semantic combinations in primate calls. *Nature* 441. 303.

Clay, Z. & K. Zuberbühler. 2011. Bonobos extract meaning from call sequences. *Plos One* 6(4). e18786.

Cook, R. 2012. The ontogenetic origins of mirror neurons: Evidence from 'tool-use' and 'audiovisual' mirror neurons. *Biology Letters* 8(5). 856–859.

Crockford, C., R. M. Wittig, R. Mundry & K. Zuberbühler. 2012. Wild chimpanzees inform ignorant group members of danger. *Current Biology* 22(2). 142–146.

Enard, W., M. Przeworski, S. E. Fisher, C. S. L. Lai, V. Wiebe, T. Kitano, A. P. Monaco & S. Päabo. 2002. Molecular evolution of FOXP2, a gene involved in speech and language. *Nature* 418(6900). 869–872.

Fitch, W. T. & K. Zuberbühler. 2013. Primate precursors to human language: Beyond discontinuity. In E. Altenmuller, S. Schmidt & E. Zimmermann (Eds.), *The evolution of emotional communication. From sounds in nonhuman mammals to speech and music in man*, 26–48. Oxford: Oxford University Press.

Gallese, V. & A. Goldman. 1998. Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences* 2(12). 493–501.

Gallese, V. & C. Sinigaglia. 2011. What is so special about embodied simulation? *Trends in Cognitive Sciences* 15(11). 512–519.

Genty, E., T. Breuer, C. Hobaiter & R. W. Byrne. 2009. Gestural communication of the gorilla (gorilla gorilla): Repertoire, intentionality and possible origins. *Animal Cognition* 12(3). 527–546. doi: 10.1007/s10071-009-0213-4

Herbinger, I., S. Papworth, C. Boesch & K. Zuberbühler. 2009. Vocal, gestural and locomotor responses of wild chimpanzees to familiar and unfamiliar intruders: A playback study. *Animal Behaviour* 78(6). 1389–1396.

Heyes, C. 2010. Where do mirror neurons come from? *Neuroscience and Biobehavioral Reviews* 34(4). 575–583.

Hobaiter, C. & R. W. Byrne. 2011. The gestural repertoire of the wild chimpanzee. *Animal Cognition* 14(5). 745–767.

Hockett, C. F. 1960. The origin of speech. *Scientific American* 203(3). 89–96.

Langergraber, K. E., K. Pruefer, C. Rowney, C. Boesch, C. Crockford, K. Fawcett, E. Inoue, M. Inoue-Muruyama, J. C. Mitani, M. N. Muller, M. M. Robbins, G. Schubert, T. S. Stoinski, B. Viola, D. Watts, R. M. Wittig, R. W. Wrangham, K. Zuberbühler, S. Pääbo & L. Vigilant. 2012. Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proceedings of the National Academy of Sciences of the United States of America* 109(39). 15716–15721.

Laporte, M. N. C. & K. Zuberbühler. 2010. Vocal greeting behaviour in wild chimpanzee females. *Animal Behaviour* 80(3). 467–473.
Liebal, K., M. Carpenter & M. Tomasello. 2010. Infants' use of shared experience in declarative pointing. *Infancy* 15(5). 545–556.
McComb, K. & S. Semple. 2005. Coevolution of vocal communication and sociality in primates. *Biology Letters* 1(4). 381–385.
Mukamel, R., A. D. Ekstrom, J. Kaplan, M. Iacoboni & I. Fried. 2010. Single-neuron responses in humans during execution and observation of actions. *Current Biology* 20(8). 750–756.
Ouattara, K., A. Lemasson & K. Zuberbühler. 2009. Wild campbell's monkeys concatenate vocalizations into context-specific call sequences. *Proceedings of the National Academy of Sciences of the United States of America* 106(51). 22026–22031.
Papworth, S., A.-S. Böse, J. Barker & K. Zuberbühler. 2008. Male blue monkeys alarm call in response to danger experienced by others. *Biology Letters* 4. 472–475.
Pika, S., K. Liebal & M. Tomasello. 2005. Gestural communication in subadult bonobos (pan paniscus): Repertoire and use. *American Journal of Primatology* 65(1). 39–61.
Rizzolatti, G. & M. A. Arbib. 1998. Language within our grasp. *Trends in Neurosciences* 21(5). 188–194.
Rizzolatti, G. & L. Craighero. 2004. The mirror-neuron system. *Annual Review of Neuroscience* 27. 169–192.
Roberts, A. I., S.-J. Vick, S. G. B. Roberts, H. M. Buchanan-Smith & K. Zuberbühler. 2012. A structure-based repertoire of manual gestures in wild chimpanzees: Statistical analyses of a graded communication system. *Evolution and Human Behavior* 33(5). 578–589.
Seyfarth, R. M., D. L. Cheney & P. Marler. 1980. Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science* 210. 801–803.
Slocombe, K. E., T. Kaller, L. Turman, S. Townsend, S. Papworth, P. Squibbs & K. Zuberbühler. 2010. Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. *Behavioral Ecological Sociobiology* 64(12). 1959–1966.
Slocombe, K. E. & K. Zuberbuhler. 2005. Agonistic screams in wild chimpanzees (pan troglodytes schweinfurthii) vary as a function of social role. *Journal of Comparative Psychology* 119(1). 67–77.
Slocombe, K. E. & K. Zuberbühler. 2006. Food-associated calls in chimpanzees: Responses to food types or food preferences? *Animal Behaviour* 72. 989–999.
Slocombe, K. E. & K. Zuberbühler. 2007. Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences of the United States of America* 104. 17228–17233.
Tomasello, M. 2008. *Origins of human communication*. Cambridge MA: MIT Press.
Tomasello, M. 2010. *Why we cooperate*. Boston: Review Books.
Townsend, S. W., T. Deschner & K. Zuberbühler. 2008. Female chimpanzees use copulation calls flexibly to prevent social competition. *PLoS One* 3(6). e2431.
Townsend, S. W., K. E. Slocombe, M. E. Thompson & K. Zuberbuhler. 2007. Female-led infanticide in wild chimpanzees. *Current Biology* 17(10). R355–R356.
Wich, S. A. & H. de Vries. (2006). Male monkeys remember which group members have given alarm calls. *Proceedings of the Royal Society B-Biological Sciences* 73(1587). 735–740.
Zuberbühler, K. 2012. Cooperative breeding and the evolution of vocal flexibility. In M. Tallerman & K. Gibson (Eds.), *Oxford handbook of language evolution*, 71–81. Oxford: Oxford University Press.